

Planktonic Copepods in a Sub-Tropical Estuary: Seasonal Patterns in the Abundance of Adults, Copepodites, Nauplii, and Eggs in the Sea Bed

NANCY H. MARCUS

Department of Oceanography, Florida State University, Tallahassee, Florida 32306

Abstract. The seasonal abundance of copepod eggs in the bottom sediments of the Apalachicola estuary was documented at bimonthly intervals between November 1989 and August 1990. Concentrations as high as 10^6 m^{-2} were noted. In addition, when bottom sediments from the estuary were incubated in the laboratory at ambient environmental conditions, large numbers of nauplii hatched, indicating that the eggs in the sediments constituted a large pool of potential recruits for the planktonic population. The eggs in the sediments and the nauplii that hatched were identified as *Acartia tonsa*, based upon morphology and the dominance of this species in the estuary. Therefore, the occurrence of copepod eggs in bottom sediments is not a phenomenon limited to temperate-boreal coastal environments.

Introduction

Estuaries are among the most productive marine systems in the world (Lauff, 1967) and as such are important nursery grounds for a wide variety of fish and invertebrates (Haedrich, 1983). Among the more important food items in the diets of these animals are copepod nauplii (Houde and Lovdal, 1984). In temperate estuaries, the appearance of copepod nauplii in the water column has been attributed to the hatch of eggs that were recently spawned by females, as well as to the hatch of eggs that were resuspended from the sea bottom, having been spawned by females some time previously (*e.g.*, Uye, 1983). The contribution of eggs in the sea bed to the naupliar population may be substantial, as concentrations as high as 10^6 m^{-2} have been documented for these ecosystems. With the exception of a study on the occurrence of eggs of *Centro-*

pages hamatus in the sea bed of Alligator Harbor, Florida (Marcus, 1989), there have been no studies of the distribution and abundance of copepod eggs in the sea bottom sediments of sub-tropical or tropical waters. The purpose of this study was to determine whether copepod eggs are as numerous in the bottom sediments of sub-tropical estuaries as they are in temperate systems, and to relate such patterns to the occurrence of naupliar, copepodite, and adult planktonic stages.

Materials and Methods

The Apalachicola estuarine system in northwest Florida ($29^{\circ} 35'N$ to $29^{\circ} 55'N$; $84^{\circ} 20'W$ to $85^{\circ} 20'W$) (Fig. 1) is typical of many sub-tropical estuarine systems found throughout the world. A recent summary of the physical, chemical, and biological characteristics of the system was provided by Livingston (1984). The system consists of East Bay, Apalachicola Bay, St. Vincent Sound, and western portions of St. George Sound. Three barrier islands that run along the extreme southern edge of the system limit the exchange of low salinity estuarine waters with the Gulf of Mexico. The Apalachicola River is the major source of fresh water to the system, followed by rainfall. As a result, East Bay is oligohaline, and the other sections grade from mesohaline to polyhaline. There are strong seasonal trends in temperature, salinity, dissolved oxygen, and turbidity. Vertical gradients of salinity are typical and reflect river flow and tidal conditions. On the other hand, thermal stratification is minimal due to wind-mixing. The average depth at mean low tide ranges from 2 to 3 m (the depth of the Intracoastal Waterway is 3.6 m). The sea bottom of the system includes areas that are extremely silty in the central portions of Apalachicola Bay and ones that are mixtures of sand and shell along the southern edge of St. George Sound.

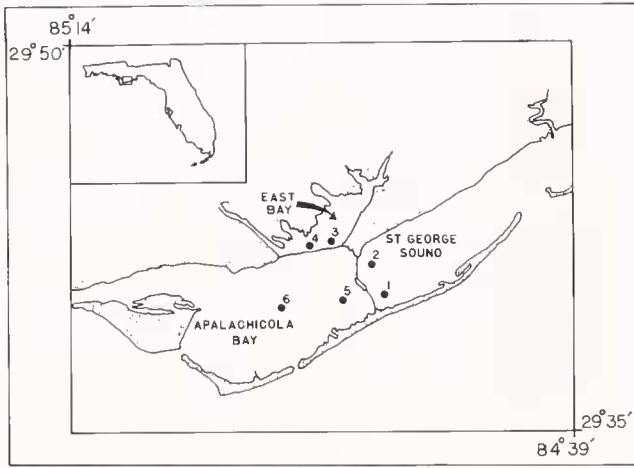


Figure 1. Location of sampling sites in the Apalachicola estuary.

The sampling program was initiated on 6 November 1989 and was continued at bimonthly intervals through 27 August 1990. Two sites were sampled in East Bay, Apalachicola Bay, and St. George Sound (Fig. 1). Their locations were chosen to represent the different salinity regimes occurring in the estuary. A complete sampling protocol involved the following: determination of surface temperature, surface and bottom salinity, and water depth; collection of two bottom cores (4.6D \times 25L cm) with a pole corer; collection of two surface-to-bottom water column samples with an expandable (2–5 m in length, 4.6 cm diameter) plastic tube; collection of plankton with a .5 m 153 μ m mesh net equipped with a General Oceanics digital flowmeter; and collection of additional surface water with a bucket. Exceptions to this scheme are the following: only one bottom core was taken at stations 3, 4, 5, and 6 in November; bottom salinity was not recorded in November; and flowmeter readings were not taken in November and January.

Surface temperature was determined with a thermometer placed in a bucket of surface water. Salinity of the same sample of water was determined with a Reichert-Jung hand-held refractometer. Bottom salinity was recorded for the top water above the sediments of one of the cores obtained from the sea bed. Depth was read off a meter scale on the pole of the coring device.

Immediately upon collection, the bottom cores were capped and stored in an insulated chest; the water column samples that were obtained with the plastic tube were filtered through a 35 μ m mesh sieve, washed into small glass jars, and preserved in 5% formalin; the plankton net samples were washed into .5 or 1 liter jars and preserved in 5% formalin; the additional surface water obtained with a bucket was filtered through a 35 μ m sieve and stored in large plastic jugs for transport.

The sediment cores were placed in a refrigerator at 5°C upon return to the laboratory. One day after collection, the upper 3 cm of each sediment core was extruded and divided at 1-cm intervals. Half of each layer was placed in a plastic screw cap test tube and preserved in 5% formalin. The eggs in these samples were extracted from the sediments and counted according to the methods of Marcus (1989). A quarter of each layer was placed in a dish with approximately 100 ml of the 35 μ m filtered water and incubated at a temperature within 3°C of the temperature at the time of collection (with the exception of the July and August collections for which the incubations were conducted at a temperature 6–7°C lower than ambient). These dishes were monitored for two days, and the nauplii that hatched were counted and preserved in 5% formalin. The filtrates obtained with the plastic tube and preserved in the field were treated with Rose Bengal upon return to the laboratory. Subsequently, the number of nauplii in each sample was determined using a dissecting microscope. The samples obtained with the plankton net and preserved in the field were examined with a dissecting microscope for the presence of different copepod species. To reduce the concentration of animals to a number manageable for counting, the material was split several times with a Folsom Plankton splitter, according to the methods of Omori and Ikeda (1984). Plankton concentrations were then calculated based upon the number of splits and the volume of water filtered. The latter value was calculated from the flowmeter readings. For the samples collected in November and January for which there were no flowmeter readings, an average of all of the filtered volumes was used in the calculations.

Although the sample sizes were small, the non-parametric Kruskal-Wallis statistical test provided by Systat was used to determine if the concentration of eggs in the sediments, nauplii in the water column, adults and copepodites of *A. tonsa* in the water column, and emergence levels of nauplii from incubated sediments differed significantly between East Bay, Apalachicola Bay, and St. George Sound. For each of these regions and for the estuary as a whole, an average and standard deviation was calculated for each parameter for each collection date.

Results

Water depths at the times of sampling ranged from 1.5 to 4.0 m. Collections in November 1989, January 1990, and August 1990 were conducted during an outgoing tide. Collections in March, May, and July 1990 were conducted on an incoming tide. Extreme high and low tides occurred in March. For each collection date, the surface temperature varied little (less than 2°C) between the different regions of the estuary (Table I). The average surface temperature for the estuary varied seasonally from 12°C in

Table I

Average surface water temperatures, and surface and bottom salinities for the different regions of the Apalachicola estuary 1989–1990

	Nov-06	Jan-03	Mar-05	May-08	Jul-10	Aug-27
Surface temperature (°C)						
St. George Sound	22 (1)	12 (0)	17 (1)	24 (0)	33 (0)	31 (0)
East Bay	22 (1)	12 (0)	17 (0)	24 (0)	32 (0)	30 (0)
Apalachicola Bay	23 (1)	12 (1)	16 (0)	24 (0)	33 (0)	32 (0)
Surface salinity (ppt)						
St. George Sound	33 (1)	21 (1)	6 (2)	24 (0)	23 (1)	22 (0)
East Bay	5 (0)	0 (0)	0 (0)	15 (0)	7 (5)	5 (0)
Apalachicola Bay	18 (18)	14 (3)	2 (1)	23 (1)	22 (4)	19 (1)
Bottom salinity (ppt)						
St. George Sound	—	21 (1)	20 (0)	24 (0)	20 (0)	27 (2)
East Bay	—	5 (1)	0 (0)	17 (1)	9 (4)	11 (1)
Apalachicola Bay	—	18 (4)	13 (1)	24 (2)	21 (3)	23 (0)

Standard deviation in parenthesis; n = 2.

January to 33°C in July. Salinity varied spatially within the system (Table I). Values as low as 0 ppt characterized the surface and bottom waters in East Bay during March, and the surface waters in East Bay during January. High values (32–33 ppt) characterized the surface waters in St. George Sound during November. The average surface and bottom salinities for the estuary varied seasonally over a range of 19 and 10 ppt, respectively.

The number of copepod eggs isolated from the sediments varied spatially and temporally (Table II, Fig. 2a). In January, the concentrations of eggs in the sediments of East Bay were significantly ($P < .05$) different than in St. George Sound and Apalachicola Bay; in May, the concentrations in St. George Sound and East Bay were significantly different ($P < .05$) from Apalachicola Bay; and in August, concentrations were significantly different ($P < .05$) in St. George Sound than in the other areas. At

the other times of the year there were no significant differences in the concentrations of eggs in the sediments in the different areas. The average concentration of eggs in the sediments of the system was highest ($4.2 \times 10^5 \text{ m}^{-2}$) in November; declined through March; increased in May; and declined to a low ($7.8 \times 10^4 \text{ m}^{-2}$) in August.

The number of nauplii that hatched from the sediments that were incubated in the laboratory varied spatially and temporally (Table III, Fig. 2b). In May, the concentrations of nauplii from the sediments of St. George Sound were significantly different ($P < .05$) than in Apalachicola Bay; and in March and July, the concentrations for East Bay were significantly different than in the other two portions of the system. The average concentrations for the system gradually declined from a maximum of $4.7 \times 10^5 \text{ m}^{-2}$ in November to a minimum of $2.4 \times 10^4 \text{ m}^{-2}$ in August.

Nauplii were always present in the water column, although their numbers varied temporally and, to a limited extent, spatially (Fig. 2c, Table IV). The average concentration for the system was high ($7.1 \times 10^4 \text{ m}^{-3}$) in November, low in January and March (1.2 to $2.0 \times 10^4 \text{ m}^{-3}$), and high again in May, July, and August (7.4 to $9.6 \times 10^4 \text{ m}^{-3}$). In November and May, the concentration of nauplii in the water column of East Bay was significantly different ($P < .05$) than in St. George Sound.

Acartia tonsa was the dominant planktonic copepod species in the estuary throughout the year, always exceeding 50% of the numerical copepod (adults and copepodites) density. *Oithona* (species not identified) accounted for 24%, 10%, and less than 5% of the numerical copepod density in March, May, and the remainder of the year, respectively; *Paracalanus* (species not identified) represented 41% of the numbers in November and less than 10% the remainder of the year. Together, these three genera accounted for 95 to 99% of copepods (adults and copepodites) throughout the year. The concentration of

Table II

Concentration of eggs (mean and standard deviation $\times 10^5$, n = number of samples) in the sediments of the different regions of the Apalachicola estuary 1989–1990

	Nov-06	Jan-03	Mar-05	May-08	Jul-10	Aug-27
St. George Sound						
Mean	7.07	2.31	1.05	2.45	1.40	1.23
SD	8.19	.89	.38	1.20	.41	.12
n	4	4	4	4	4	4
East Bay						
Mean	.32	5.03	.82	4.05	2.40	.53
SD	.25	1.46	.23	1.78	1.40	.22
n	2	4	4	4	4	3
Apalachicola Bay						
Mean	2.39	1.47	1.02	1.15	.75	.52
SD	1.30	.78	.38	.24	.32	.10
n	2	4	4	4	4	4

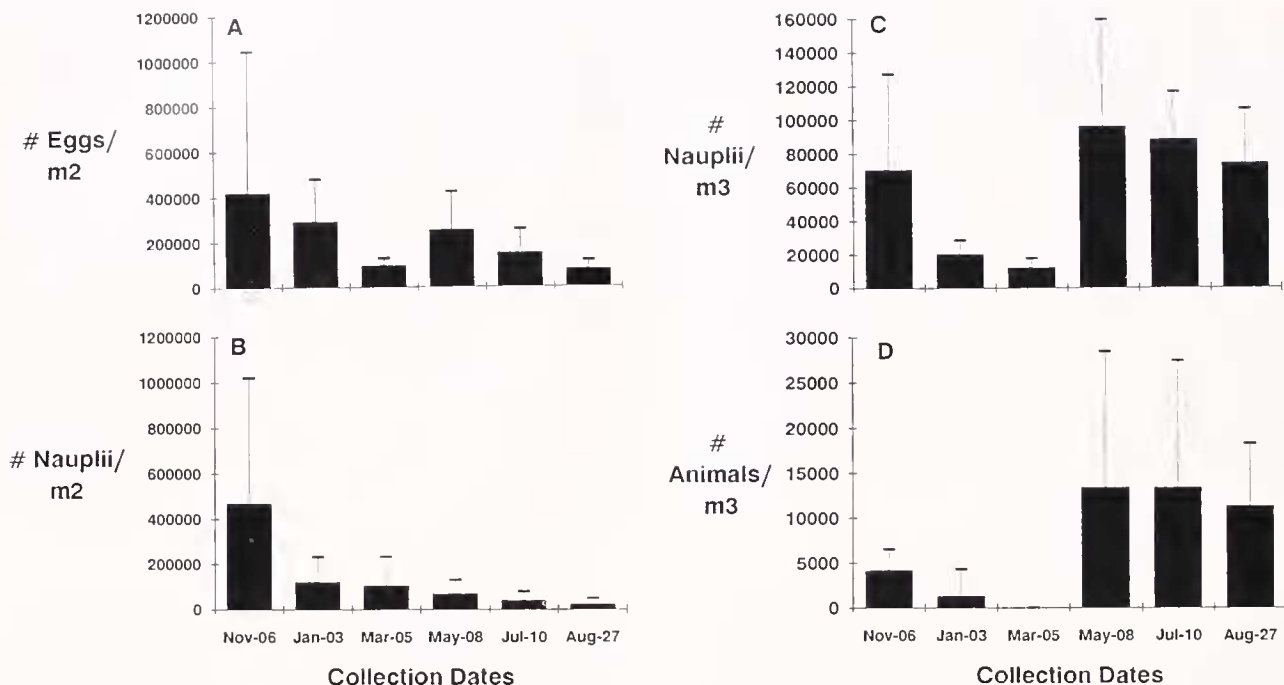


Figure 2. Seasonal trends of (A) resting egg concentrations in the sea bed, (B) numbers of nauplii emerging from sediments incubated in the laboratory, (C) nauplii concentrations in the water column, and (D) adult and copepodite concentrations in the Apalachicola estuary. Mean and standard deviation.

adults and copepodites of *A. tonsa* did not differ significantly between the three regions of the system. The average concentration of adults and copepodites of *A. tonsa* in the estuary varied seasonally, being moderately high ($4.2 \times 10^3 \text{ m}^{-3}$) in November, low ($1.3 \times 10^3 \text{ m}^{-3}$) in January, extremely low (13 m^{-3}) in March, and then high (1.1 to $1.3 \times 10^4 \text{ m}^{-3}$) in May, July, and August (Fig. 2d).

Discussion

For most of the year, the average concentration of copepod eggs in the sea bed of the Apalachicola estuarine system was of the same order of magnitude (10^5 m^{-2}) as that reported for *Centropages hamatus* in Alligator Harbor, Florida (Marcus, 1989). These values for sub-tropical systems are equivalent in magnitude to the values reported for temperate bays and estuaries (e.g., Kasahara *et al.*, 1975; Uye 1983). In the present study, the emergence of large numbers of nauplii (average 2.4×10^4 – $4.7 \times 10^5 \text{ m}^{-2}$) from the sediments that were incubated in the laboratory at ambient field conditions indicated that large numbers of these eggs were viable. At such concentrations and levels of emergence, these eggs constitute a large potential source of naupliar recruits for the planktonic population and a large potential source of prey items for larval fish and invertebrates. Because the eggs isolated from the sediments of the Apalachicola system and those spawned

by *Acartia tonsa* females in the laboratory are morphologically similar, and because *A. tonsa* is the numerically dominant copepod in the system, then most of the eggs isolated from the sediments, as well as the nauplii that emerged from the sediments, were probably *A. tonsa*. Eggs of *Oithona* and *Paracalanus*, the two other genera that were numerically prominent in the estuary, have never been reported from the sea bed of any system that has been studied. In the case of *Oithona*, the females carry their eggs in sacs attached to their bodies. Although females of *Paracalanus spp.* shed their eggs into the water column, the eggs may be too fragile to withstand mixing into the sediments. The salinity regimes of East Bay, St. George Sound, and Apalachicola Bay conformed to their designations as oligohaline, mesohaline, and polyhaline. However, a comparison of the concentration of eggs in the sediments, nauplii in the water column, adults and copepodites of *A. tonsa* in the water column, and emergence levels of nauplii from incubated sediments revealed no or only a few significant differences among the regions. These results may reflect the tolerance of *A. tonsa* to a wide range of salinities (Day *et al.*, 1989).

Since the initial discovery of calanoid copepod eggs in sea bottom sediments of temperate coastal waters (Kasahara *et al.*, 1974), eggs of planktonic copepods that have been isolated from the sea bed have typically been referred to as resting or dormant. Grice and Marcus (1981) dis-

Table III

Concentration of naupli (mean and standard deviation $\times 10^5$, n = number of samples) emerged from sediments incubated in the laboratory from the different regions of the Apalachicola estuary 1989-1990

	Nov-06	Jan-03	Mar-05	May-08	Jul-10	Aug-27
St. George Sound						
Mean	4.13	1.83	1.87	1.24	.20	.08
SD	4.28	1.24	1.36	.61	.12	.06
n	4	4	4	4	4	4
East Bay						
Mean	1.08	1.08	.01	.70	.80	.39
SD	.03	1.24	.01	.39	.43	.30
n	2	4	4	4	4	4
Apalachicola Bay						
Mean	9.44	.75	1.31	.15	.18	.23
SD	9.23	.72	1.26	.08	.14	.25
n	2	4	4	4	4	4

tinguished two types of resting or dormant eggs: diapause eggs and quiescent subitaneous eggs. Diapause eggs undergo a mandatory arrest of development, during which development does not resume even if conditions are suitable. Subitaneous eggs can develop without delay, but if they are exposed to unsuitable conditions (*e.g.*, low temperature or oxygen) development is delayed and they become quiescent. Unlike diapause eggs, quiescent subitaneous eggs resume development immediately upon re-exposure to suitable conditions. Despite these differences, both types of resting eggs are functionally similar in terms of their impact on population growth, because both introduce a lag phase into the life cycle. In the present study, experiments were not conducted to determine whether the resting eggs that were isolated from the sea bed of the Apalachicola estuary were diapause or quiescent subitaneous eggs.

The seasonal trend observed in this study (Fig. 2d), in the abundance of adults and copepodites of *Acartia tonsa*,

was similar to that previously reported for the Apalachicola system (Edmiston, 1979). Although the species was present throughout the year, the concentration of adults and copepodites cycled from high values in the spring and summer to low values in the fall and winter. On the other hand, the greatest concentration of eggs in the sediments occurred in the fall following the spring and summer peak of adults and copepodites. A similar phased relationship between the concentrations of eggs in the sediments and adult concentrations in the water column was reported for several species of copepods in the Inland Sea of Japan (Kasahara *et al.*, 1975). For these species, the hatch of resting eggs was crucial to their perpetuation in as much as the planktonic stages disappeared entirely from the water column for a portion of the year. Although the planktonic stages of *A. tonsa* did not disappear entirely from the Apalachicola estuary, they did undergo a marked seasonal cycle in abundance. The presence of eggs in the sediments suggests that these stages may provide an im-

Table IV

Concentration of nauplii (mean and standard deviation $\times 10^5$, n = number of samples) in the water column of the different regions of the Apalachicola estuary 1989-1990

	Nov-06	Jan-03	Mar-05	May-08	Jul-10	Aug-27
St. George Sound						
Mean	.26	.22	.12	1.02	.81	.95
SD	.21	.08	.02	.33	.16	.42
n	4	4	4	4	4	4
East Bay						
Mean	1.23	.15	.14	.50	.78	.73
SD	.66	.05	.05	.20	.21	.13
n	2	4	4	4	4	4
Apalachicola Bay						
Mean	.64	.24	.09	1.36	1.07	.55
SD	.21	.10	.08	.91	.39	.27
n	2	4	4	4	4	4

portant source of recruits for the planktonic population especially during the Spring.

Although Reeve (1975) pointed out the potential importance of benthic resting stages in discussing the zooplankton of shallow sub-tropical lagoonal systems of southern Florida, and Tranter and Abraham (1971) suggested that a benthic diapause phase might be the basis of the seasonal replacement of several *Acartia* species in the Cochin backwater in India, the actual presence of such stages in sub-tropical systems had not been demonstrated. The results of Marcus (1989) on *Centropages hamatus* and this study on *Acartia tonsa* provide strong support for the hypotheses of Reeve and of Tranter and Abraham, for the existence of copepod resting eggs in the sea bed of sub-tropical estuaries is now evident.

Acknowledgments

I thank Teresa Donelan, Robert Lutz, Denise Miller, and Keith Taulbee for their assistance in the field and laboratory and two anonymous reviewers for their suggestions regarding the manuscript. Research supported by NOAA Grant NA89AA-D-CZ146 and NSF Grant OCE87-22922. Contribution Number 1062 of the Florida State University Marine Laboratory.

Literature Cited

- Day, J. W., C. Hall, W. M. Kemp, and A. Yanez-Arancibia. 1989. *Estuarine Ecology*. John Wiley and Sons, New York. 558 pp.

- Edmiston, L. 1979. *The Zooplankton of the Apalachicola Bay System*. M.S. Thesis. Florida State University. 104 pp.
- Grice, G., and N. Marcus. 1981. Dormant eggs of marine copepods. *Oceanogr. Mar. Biol. Ann. Rev.* **19**: 125-140.
- Haedrich, R. 1983. Estuarine fishes. Pp. 183-208 in *Estuaries and Enclosed Seas*, B. H. Ketchum, ed. Elsevier, Amsterdam.
- Houde, E. D., and J. A. Lovdal. 1984. Seasonality of occurrence, foods and food preferences of ichthyoplankton in Biscayne Bay, Florida. *Estuarine Coast. Shelf Sci.* **18**: 403-419.
- Kasahara, S., S. Uye, and T. Onbé. 1974. Calanoid copepod eggs in sea-bottom muds. *Mar. Biol.* **26**: 167-171.
- Kasahara, S., S. Uye, and T. Onbé. 1975. Calanoid copepod eggs in sea-bottom muds. II. Seasonal cycles of abundance in the populations of several species of copepods and their eggs in the Inland Sea of Japan. *Mar. Biol.* **31**: 25-29.
- Lauff, G. H., ed. 1967. *Estuaries*. AAAS Publication # 83, Washington, DC.
- Livingston, R. J. 1984. The ecology of the Apalachicola Bay system: an estuarine profile. *U. S. Fish. Wildl. Serv. FWS/OBS* 82/05. 148 pp.
- Marcus, N. H. 1989. Abundance in bottom sediments and hatching requirements of eggs of *Centropages hamatus* (Copepoda:Calanoida) from the Alligator Harbor region, Florida. *Biol. Bull.* **176**: 142-146.
- Omori, M., and T. Ikeda. 1984. *Methods in Marine Zooplankton Ecology*. John Wiley and Sons, New York. 322 pp.
- Reeve, M. R. 1975. The ecological significance of the zooplankton in the shallow subtropical waters of south Florida. Pp. 352-371 in *Estuarine Research*, Vol. 1, L. E. Cronin, ed. Academic Press, New York.
- Tranter, D. J., and S. Abraham. 1971. Coexistence of species of *Acartiidae* (Copepoda) in the Cochin Backwater, a monsoonal estuarine lagoon. *Mar. Biol.* **11**: 222-241.
- Uye, S. 1983. Seasonal cycle in abundance of resting eggs of *Acartia steuri* Smirnov (Copepoda:Calanoida) in sea-bottom mud of Onagawa Bay, Japan. *Crustaceana* **44**: 103-105.